Quantitative Relationships between Fleas and Rodents in a Hawaiian Cane Field[1]

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ABSTRACT: Relative numbers of *Xenopsylla vexabilis* Jordan on *Rattus exulans* (Peale) and *Mus musculus* L. and in their nests were determined monthly in a field of maturing sugar cane at Kukuihaele, island of Hawaii, January 1962–March 1963, in a preliminary study using nest boxes and live traps. Mean numbers of fleas in active rat nests were most closely correlated with mean numbers of fleas infesting rats when they were cage-trapped in the previous month. Mean numbers of fleas in active mouse nests were most closely correlated with mean numbers of mice that had been recorded per mouse nest found occupied in the previous month. Ratios of mean number of fleas on trapped rats to mean number of fleas in rat nests the following month averaged .20 when means increased and .30 when they decreased. When the total flea index was substituted for mean number of fleas in nests, ratios averaged .32 when fleas became more abundant and .36 when they decreased in numbers. Further study of fleas in rat nests is needed before predictions of flea abundance are routinely made from fleas counted on trapped rats.

TO OBTAIN A MEASURE of rodent-flea abundance, the plague surveillance program in Hawaii has emphasized trapping rodents rather than excavating burrows for nests because monthly systematic excavation is not feasible in the fields of sugar cane that cover most of the enzootic plague area on the Hamakua Coast. Basic studies by Eskey (1934) on the epidemiology of plague were concerned with area-wide quarterly abundance of fleas on rodents, but not in nests. Flea and rodent populations can vary greatly in both space and time in Hamakua. Therefore, it would seem ideal to ascertain the mean number of fleas in nests in a small, relatively uniform area such as a cane field, and to relate this number in some way to the mean number of fleas on routinely trapped rodents in that field so that accurate predictions of total flea abundance or scarcity, or at least the mean number of fleas in nests, could be made for any particular field that is under surveillance by routine trapping only. Hence, the objective of this preliminary study was to obtain data sufficiently homogeneous for meaningful analyses of correlation and regression leading to identification of cause and effect relationships of predictive value in the Hamakua District, Hawaii. Success was limited; consequently, the results will have more academic interest for ecologists than immediate practical value to plague surveillance personnel.

MATERIALS AND METHODS

Location and Description of the Study Area

Cane field 101b of the Honokaa Sugar Company, Hamakua District, island of Hawaii, was selected as the study area because the last isolation of the plague bacillus in Hawaii was made from fleas collected there in May 1957. This 15.4-ha field (Fig. 1) lies in the corner formed by the Pacific Ocean on the north and Waipio Valley on the west. The village of Kukuihaele borders on the east. Elevation ranges from 220–300 meters, and slope is 12–20 per cent. Roads and gulches fragment the field. The

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deepest gulch has many rock outcrops and trees; other gulches are less rocky and have a ground cover of grass, forbs, and shrubs. The soil is a reddish, granular humic latosol in the Lalakea silty clay loam series. Haas (1965*b*) described certain climatic and microclimatic conditions of the area and cited literature describing the district.

Culture of Sugar Cane

After harvest in May 1961 of a third crop (second ratoon) from a planting made about 6 years previously, the field was plowed. A new crop (plant cane) was planted during the period June 30–July 12, 1961, and the main part of this study was conducted during growth of this crop. In February 1962 a mixture of Dalapon, Karmex, and Atrazine in oil was applied to weeds among the cane plants. In March 1962 a fertilizer containing 61% K_2O was applied. In May 1962 weeds were hoed by hand. There was no irrigation despite a severe drought. Harvest was in May 1963 when the cane was slightly over 22 months old.

Traps and Trapping

A 54-trap grid of cage-type live traps was located in the northwest 3.2-ha fragment of the field (Fig. 1). Traps were 15.2 meters apart in six parallel rows of nine traps each. Monthly, beginning in October 1961, when the cane was 3 months old, traps were set for 4 consecutive nights with fresh coconut bait. April 1963 was the last month of trapping. Rodents caught in the cage traps were released in the field, but fleas combed from trapped hosts were killed in the plague surveillance laboratory. Rodents trapped the first time were marked by clipping off the tip of an ear.

Data obtained earlier on rodents and fleas, that is, during growth of the ratoon crop harvested in May 1961, were essential as well as supplemental to this later study. Two 54-trap grids of live traps had been set for 4 consecutive nights monthly from July 1959 through March 1961. One grid was in the same location as the single one during growth of the 1961–1963 crop. The second grid overlapped the area covered by the south half of the westernmost box grid (Fig. 1). Flea indices were of value in making comparisons between crops, but rodent population density estimates (Tomich,[3] unpublished manuscript) were essential because only during growth of the 1959–1961 crop were live-trapped rodents marked with coded ear tags, enabling densities to be estimated directly by Hayne's (1949) modified Lincoln Index. These density estimates had very high correlations with unmarked rats trapped ($r = 0.97$, $P < .001$) and with unmarked plus marked mice trapped ($r = 0.77$, $P < .01$). Therefore, densities in the 1961–1963 cane crop were worked out indirectly by proportions using as one side of the equation: mean number trapped (1959–1961) divided by the mean of the corresponding Lincoln Index estimates. Estimations of monthly mean numbers of active rodent nests were then possible (Haas, 1966*b*). Nest densities were necessary for estimations of monthly total flea indices. The respective index for *Rattus exulans* became part of a ratio considered in this report. To maximize accuracy of correlations, however, direct monthly total counts of unmarked rodents live-trapped during 1961–1963 represented rodent population densities in the cane field.

Nest Boxes

Figure 1 shows locations of the three 20-unit grids of subterranean nest boxes. Half of the boxes (30) were designed for mice, and half for rats. Haas (1966*b*) gave detailed descriptions of these boxes, their arrangement and inspection schedule, and how rodents and fleas inhabiting them were studied. A brief redescription of box arrangement is as follows: The two parallel rows of boxes in each grid were 30.5 meters apart. The boxes were only 15.2 meters apart in each row, but as boxes for the two species of rodents alternated in an identical sequence in each row, boxes for each species were not less than 30.5 meters apart.

Fleas, rodents, and nests were treated as follows: Nests with their flea and rodent inhabitants, if any, were sampled monthly with replacement. First, rodents were captured and fleas were combed from the pelage. Next, the nests were removed, bagged, and carried to the laboratory where adult fleas and larvae were

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collected with modified Berlese funnels. After brief study in the laboratory, all fleas were returned to their respective nests and hosts. Nests were replaced in their respective boxes before being reinfested with their fleas, but rodents were reinfested with their fleas before being returned to their nests in the boxes. For identification purposes all rodents captured in nest boxes were marked by toe clipping or with metal ear tags; fleas were not marked. Nests termed "occupied" contained rodents when the nest boxes were inspected. Nests termed "active" include not only occupied ones but those that showed fresh sign of occupancy, such as new construction, a smooth floor surface, and presence of flea larvae or fed adults. Rodents captured in nest boxes are not referred to as "trapped" or "live-trapped" rats or mice. Only those animals caught in cage traps are so designated.

Statistical Methods

To increase smaller sample sizes and to smooth curves for more precision in data analyses, 3-month moving means of numbers of fleas, rodents, and nests were calculated. This method also had some normalizing effect on distribution of means and significantly strengthened correlations. Numbers of rodents in nests and of fleas on rodents and in nests had skewed distributions not fitting the Poisson. Except for the t-test of significance between mean numbers of fleas on live-trapped rats, data were not transformed because attention here was on original scale means ($\bar{x}$) instead of distributions having these measures of central tendency. Furthermore, relationships of population densities rather than rates of change were under study, correlation coefficients were higher with original scale data, and original scale means already had linear relationships.

RESULTS

Numbers and Kinds of Fleas, Rodents, and Nests Examined

Only one species each of flea, rat, and mouse was sufficiently abundant to study in detail. They

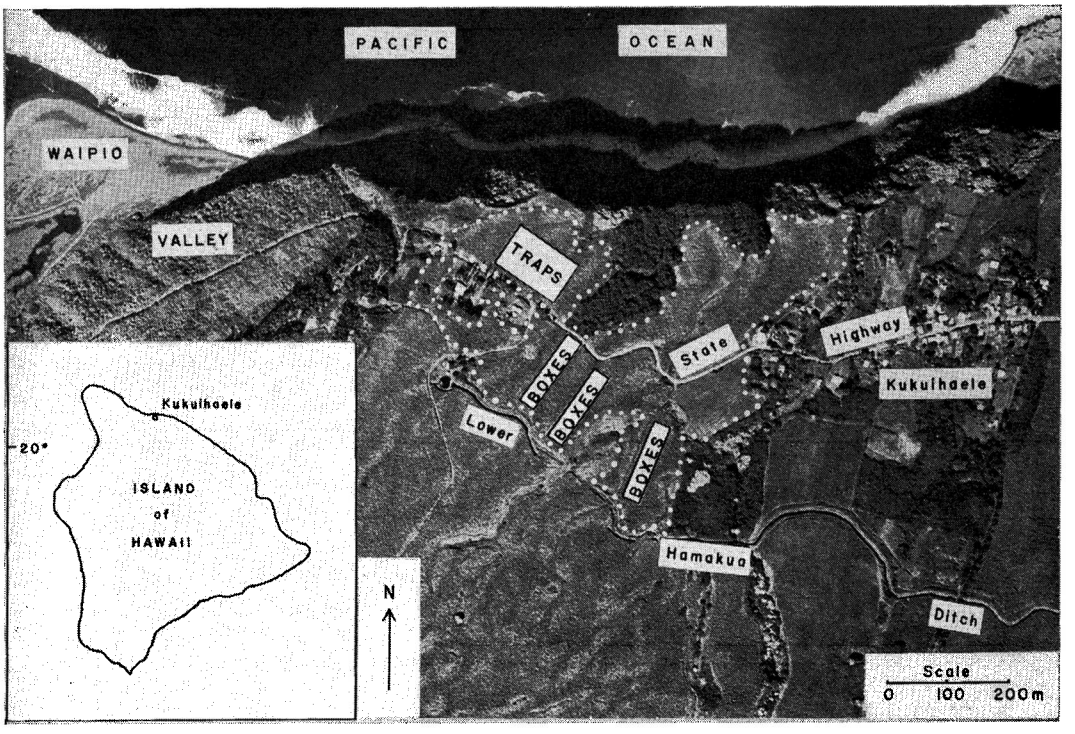

FIG. 1. Aerial photograph showing cane field 101b of the Honokaa Sugar Co., Hamakua District, island of Hawaii, with locations of cage traps and nest boxes during the 1961–1963 crop. (R. M. Towill Corp. photograph.)

were *Xenopsylla vexabilis* Jordan, *Rattus exulans* (Peale), and *Mus musculus* L., respectively. The other naturally occurring flea, *Leptopsylla segnis* (Schönherr), and the other rodent, *R. rattus* (L.), were so scarce during July 1961–April 1963 that data for them are not considered in this report.

Figure 2 shows the mean numbers of *X. vexabilis* per rodent and nest. Marked *R. exulans* were excluded from live-trapped samples because, contrary to results with marked *M. musculus,* permanent removal of fleas significantly ($P < .01$) depressed the mean number per rat. Haas (1966*b*) discussed aspects of the nest-box technique that affect estimates of total numbers of fleas.

Of active rat nests, 69% were infested with *X. vexabilis* adults and 34% with larvae, probably of the same species. For mouse nests respective data were 45% and 21%.

Monthly mean numbers of female fleas in rat nests graphed similarly to means (of both sexes combined) in Figure 2, but the magnitudes of the two peaks were reversed, with 3.9 fleas in summer and 5.1 fleas in winter. From August through October densities were almost constant at about 2 fleas per nest.

Sex ratios of *X. vexabilis* indicated population samples consisted of 60% males: May–August in *R. exulans* nests; June–September in *M. musculus* nests. In September the percentage of males in rat nests began a decline toward a low of 32% in October. In contrast, the percentage in mouse nests increased in October and reached a peak of 75% in November. Next, a trend toward convergence occurred with the

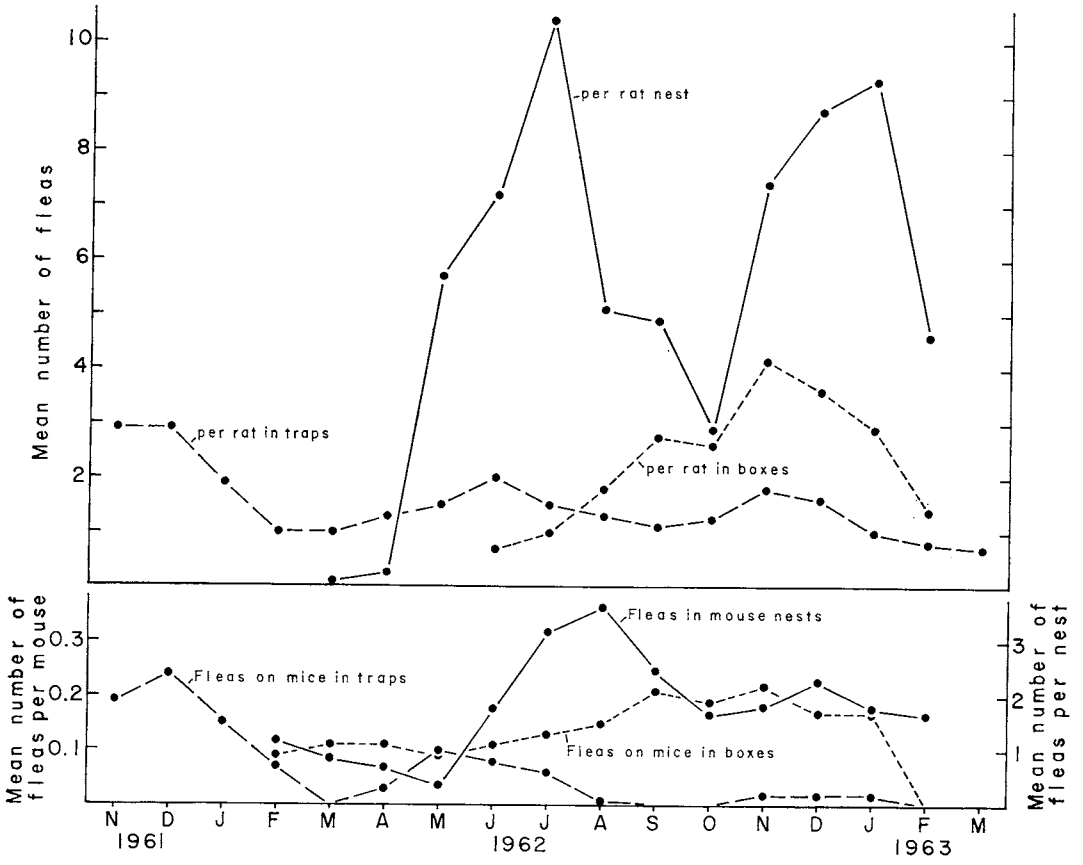

FIG. 2. Mean numbers of *Xenopsylla vexabilis* per *Rattus exulans* and *Mus musculus* captured outside and within nest boxes, and per active nest in nest boxes in cane field 101b, Kukuihaele, Hawaii; 3-month moving means. Marked *R. exulans* excluded from live-trapped samples. Nestling rodents excluded from samples from nest boxes.

percentage of males in rat nests leveling off at 44% for the period November 1962–February 1963, and in mouse nests dropping steeply to 54% by February. For the entire study, the percentage of male fleas in rat nests was 48%, and in mouse nests 62%. Percentages in samples of fleas from hosts are not presented because all monthly totals of fleas were below 100. Even in mouse nests, only in July and August were there more than 99 fleas, suggesting that large chance variations affected the sex ratios. Rat nests in the 10-month period from May through February contained 100+ fleas each month except August and October (3-month moving totals).

Means in Figure 2 were calculated in part from data in Table 1. The monthly numbers of *R. exulans* during February–June 1962 were so small that a significant difference could not be detected between the high mean number of fleas in June and low means in February–March and September.

Of 30 rat and 30 mouse nest boxes, 20 and 28, respectively, were nested in one or more times. Of active nests (Table 1), 33% belonging to rats were occupied at inspection compared with 52% of mouse nests. Mice built nearly 20% of their nests in antechambers. With one exception such nests were destroyed eventually and replaced with a new one in the nest chamber, but the high percentage of antechamber nests suggests that the nest chamber was too large for mice. Ball-type mouse nests that filled nest chambers were larger than those excavated from burrows during concurrent studies. Fleas might have been handicapped by the extreme bulk of the nest in relation to host size.

Both rat and mouse nests were constructed of strips torn from the edges of cane leaves. Occasionally rootlets and other plant materials were added. Nests ranged from small, simple, and scanty to large, complex, and dense.

Of 27 different nestling, juvenile, and adult individual rats recorded in boxes during the study, 41% were captured only once. Excluding nestlings as in Table 1, grand totals of counts of unmarked plus marked rats but excluding repeats (that is, rats captured a second time in the same month) were 22 ♂♂ and 17 ♀♀. One ♂ and one ♀ each were found in two different

TABLE 1

NUMBER OF *Rattus exulans*, *Mus musculus*, AND ACTIVE NESTS EXAMINED IN CANE FIELD 101b, KUKUIHAELE, HAWAII, 1961–1963 (3-MONTH MOVING TOTALS)

	R. exulans			*M. musculus*		
MONTH	IN TRAPS[a]	IN BOXES[b]	NESTS EXAMINED	IN TRAPS[c]	IN BOXES[b]	NESTS EXAMINED
Nov	22(43)	—	—	21	—	—
Dec	24(50)	—	—	21	—	—
Jan	17(32)	0[d]	0[d]	13	8[d]	9[d]
Feb	8(23)	1	1	14	11	12
Mar	8(20)	1	7	15	18	19
Apr	6(16)	2	12	33	18	24
May	6(12)	4	18	59	33	37
Jun	4(7)	6	17	84	61	42
Jul	13(23)	8	16	92	71	41
Aug	15(26)	11	17	96	65	42
Sep	14(27)	12	22	70	40	41
Oct	16(27)	11	31	56	42	45
Nov	21(42)	13	37	57	32	42
Dec	23(55)	15	37	58	24	37
Jan	20(62)	20	35	57	12	30
Feb	14(50)	12	28	38	14	20
Mar	11(36)	7[d]	18[d]	53	9[d]	13[d]

[a] Unmarked rats; marked + unmarked rats in parentheses.
[b] Nestlings excluded.
[c] Marked + unmarked mice.
[d] Two-month total.

boxes in one month. Rats seen more than once during the study usually moved to a box farther away than the nearest one. The longest movement was 105 meters. No rat was found in more than two different boxes, nor more than 3 times, nor over a period exceeding 5 months. Three litters of *R. exulans* nestlings were found in the period May–June.

Of 124 different nestling, juvenile, and adult individual mice recorded in boxes during the study, 57% were captured only once. Again excluding nestlings, grand totals of counts of unmarked plus marked mice but excluding repeats were 75 ♂ ♂ and 68 ♀ ♀. Repeats totaled 3 ♂ ♂ and 10 ♀ ♀. Mice seen more than once during the study were usually in the same box or in an adjacent one. The longest movement was 76 meters. Only 2 mice were found in as many as three different boxes. The maximum number of captures of the same mouse was 6, and the longest period between first and last capture was 9 months. The majority of 8 litters was born during May–September. Some aggregations of mice, such as 2 adult ♂ ♂ in the same box, were unexpected, but another study (Crowcroft and Rowe, 1963) indicates this is not uncommon in *M. musculus*. Calculations from data in Table 1 show that except in February 1962 and January 1963, mice always averaged larger aggregations per active nest than rats.

A very small male *R. exulans* entered an occupied(?) mouse box through the rat excluder. A pair of *R. exulans* bypassed the excluder by penetrating a rotten tube on another mouse box to enter and nest. Mice were never found in rat boxes. One mouse was captured in an empty box. All other rodents were in boxes with nests. There was no record of the same rodent being caught in both a box and a trap. Rodent ecology in Hawaiian cane fields is treated in detail elsewhere (Tomich, unpublished manuscript).

Correlations and Regressions

Main features of rat correlation data (Table 2) are briefly as follows: The only variable significantly correlated ($P < .01$) with the mean number of fleas per active rat nest (one month lag) was the mean number of fleas per live-trapped, unmarked rat (Fig. 3). If only female fleas were counted, correlation was reduced ($r = 0.61$, $P < .05$). As for correlations between concurrent variables, the only rat population-density measurement that correlated ($P < .05$) with the mean number of fleas per active rat nest was the mean number of rats (nestlings excluded) per active nest. The mean number of unmarked, live-trapped rats did not correlate significantly with either of these last two variables but did so very strongly ($P < .001$) with the mean number of active nests.

Main features of mouse correlation data (Table 3) are briefly as follows: The variable having the strongest correlation ($P < .01$) with the mean number of fleas per active nest (one month lag) was the mean number of mice (nestlings excluded) per occupied nest (Fig. 4). As for correlations between concurrent variables, the mean number of fleas in active mouse nests was significantly correlated with the mean numbers of unmarked, live-trapped mice ($P < .02$), mice (nestlings excluded) per active nest ($P < .05$), and mice per occupied nest ($P < .01$). The mean number of unmarked, live-trapped mice did not correlate significantly with the mean number of mice per active nest but had strong correlation ($P < .01$) with the mean number of active nests.

In relating some of the same variables from rats and mice to one another, positive correlations occurred with mean numbers of fleas per active nest ($P < .05$), per rodent (nestlings excluded) captured in boxes ($P < .01$), and per trapped rodent (marked rats excluded) ($P < .001$). The percentage of male fleas in nests was negatively correlated, but not significantly. Numbers of trapped rodents were not significantly correlated. Nestlings were excluded from analyses because fleas were never observed on them.

Correlation coefficients and levels of their significance should be considered comparative rather than absolute because application of 3-month moving means rounded small random fluctuations in the original data to reveal curves that correlate strongly. Values of r in Figures 3 and 4, for example, equalled only 0.29 ns and 0, respectively, when original monthly data were tested.

Lack of correlation between mean numbers of fleas and either temperature or rainfall is apparent by inspection of data in Figure 2 and those of Haas (1965*b*). Total (absolute) flea

TABLE 2

SIMPLE CORRELATIONS CONCERNING MONTHLY MEAN NUMBERS OF *Rattus exulans*, ITS NESTS, AND *Xenopsylla vexabilis* IN CANE FIELD 101b, KUKUIHAELE, HAWAII, MARCH 1962–FEBRUARY 1963 (3-MONTH MOVING MEANS)

	VARIABLE	2	3	4	5	6	7	8
1a	Fleas/active nest	ns	0.58[a]	ns	0.60[a]	ns	ns	0.64[a]
1b	Var. 1a with 1-month lag[b]	0.86[c]	—	—	ns	ns	ns	—
2	Fleas/unmarked rat trapped	—	ns	ns	—	—	—	—
3	Fleas/rat captured in boxes		—	—	—	—	—	—
4	Unmarked rats live-trapped			—	ns	0.77[c]	0.85[d]	0.80[c]
5	Rats/active nest				—	ns	ns	—
6	Rats/occupied nest					—	0.82[c]	0.60[a]
7	Active nests						—	0.77[c]
8	Occupied nests							—

[a] $P < .05$.
[b] Correlation based on only 11 consecutive monthly observations; all other correlations based on 12.
[c] $P < .01$.
[d] $P < .001$.

TABLE 3

SIMPLE CORRELATIONS CONCERNING MONTHLY MEAN NUMBERS OF *Mus musculus*, ITS NESTS, AND *Xenopsylla vexabilis* IN CANE FIELD 101b, KUKUIHAELE, HAWAII, FEBRUARY 1962–FEBRUARY 1963 (3-MONTH MOVING MEANS)

	VARIABLE	2	3	4	5	6	7	8
1a	Fleas/active nest	ns	ns	0.66[a]	0.57[b]	0.77[c]	ns	ns
1b	Var. 1a with 1-month lag[d]	ns	—	—	0.67[b]	0.80[c]	0.75[c]	—
2	Fleas/mouse trapped[e]	—	ns	ns	—	—	—	—
3	Fleas/mouse captured in boxes		—	—	—	—	—	—
4	Unmarked mice live-trapped			—	ns	0.67[a]	0.72[c]	ns
5	Mice/active nest				—	0.70[c]	ns	—
6	Mice/occupied nest					—	0.63[b]	0.57[b]
7	Active nests						—	ns
8	Occupied nests							—

[a] $P < .02$.
[b] $P < .05$.
[c] $P < .01$.
[d] Correlation based on only 12 consecutive monthly observations; all other correlations based on 13.
[e] Marked and unmarked mice combined.

indices, calculated from data of Haas (1966*b*), likewise do not correlate with these two variables. These results do not mean that warmth, whether from summer sun or rodent body, was absolutely neutral in its effects on *X. vexabilis* activities in subterranean nests of field 101b, which lies at about the mean elevation of the enzootic plague area, and possibly of the range of the flea as well. But temperature was not a significant separate factor in the analyses of population data in this study because mean monthly soil temperatures had a range of only 19°–23.5°C (Haas, 1965*b*), and, furthermore, in nests the mean amount of heat given off by rodents is in part intrinsic in the mean densities of the inhabiting rodent populations.

Ratios Between Certain Flea Indices

With a 1-month lag in the mean number of fleas per rat nest, the ratio of mean number of fleas per trapped rat to mean number per active nest averaged .20 when the means increased and diverged. Conversely, when the same measurements decreased and converged, the ratio increased to .30 which was significantly higher ($P < .05$). The 95% CI for .30–.20, $.10 \pm .07 = (.03, .17)$. When the ratio was the mean number of fleas on trapped rats to the total flea

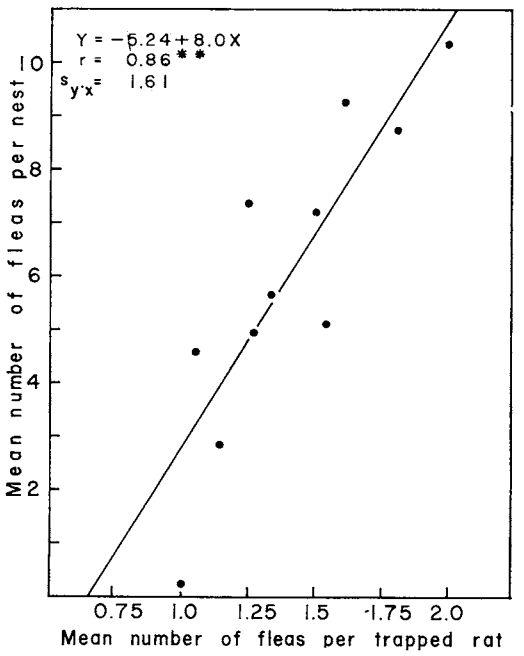

FIG. 3. Relation between mean number of *Xenopsylla vexabilis* per live-trapped, unmarked *Rattus exulans* and mean number of *X. vexabilis* per active *R. exulans* nest in nest boxes one month later; 11 pairs of 3-month moving means, March 1962 (fleas on rats)–February 1963 (fleas in nests); cane field 101b, Kukuihaele, Hawaii.

** Significant correlation ($P < .01$).

index for rats in the field (Haas, 1966*b*) during the following month, the results were .32 when fleas became more numerous, in slight contrast ($P > .05$) to .36 when fleas became less numerous. The 95% CI for these ratios were (.29, .35) and (.24, .48), respectively.

DISCUSSION

Numbers and Kinds of Fleas, Rodents, and Nests Examined

First let us account for the presence of fleas and rodents after mechanical havesting of cane followed by plowing has devastated the habitat. Some surviving rodents can be trapped in newly plowed and planted fields (Tomich, manuscript), but occupied burrows have not been found. Results of experiments using nest boxes suggest that only after several months (7 for *M. musculus*, 8 for *R. exulans*) following planting do rodents begin to burrow and nest within a new field. They bring fleas with them, evidently from nests outside the field. Subsequent generations of both rodents and fleas are probably produced mostly in nests in the field by these first invaders and their progeny.

Fluctuations in numbers of the rat flea *X. vexabilis* in nests, as discussed under correlations, were closely related to numbers of hosts (nestlings excluded) per nest. Breeding by rodents was mainly responsible for increased numbers of hosts per nest. Mortality probably accounted for most decreases. Causes of fluctuations in rodent numbers in Hawaii are treated in detail elsewhere (Tomich, manuscript).

Population densities of both rodents were low relative to those of previous years (Tomich, manuscript), and there were too many boxes for the low population density of rats (Haas, 1966*b*). Spacing between rat boxes should have been doubled. But numbers of boxes accepted evidently was dependent not only on rodent numbers, but also on availability of nest-build-

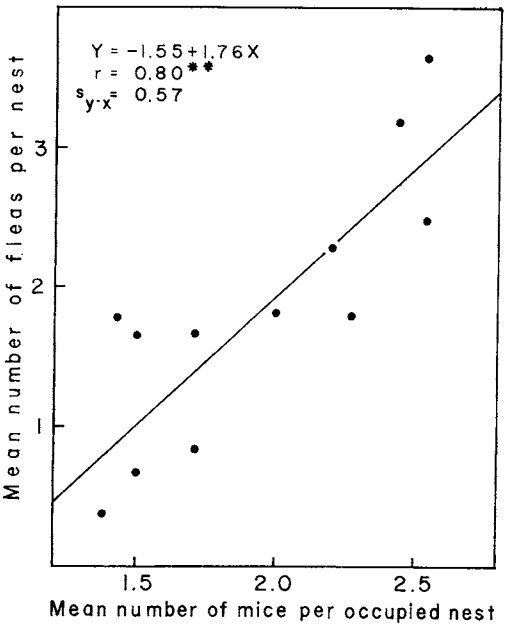

FIG. 4. Relation between mean number of *Mus musculus* (excluding nestlings) per occupied nest and mean number of *Xenopsylla vexabilis* per active mouse nest in nest boxes one month later; 12 pairs of 3-month moving means, February 1962 (mice)–February 1963 (fleas): cane field 101b, Kukuihaele, Hawaii.

** Significant correlation ($P < .01$).

ing materials, cover, and food. That is, more rats visited the field while the boxes were buried and soon after, and fewer came later, yet nesting did not occur at the time of the higher, earlier counts when the cane was only 6 or 7 months old (Table 1).

The mean number of fleas on hosts captured in boxes was usually higher than on trapped hosts probably because, when captured, many had just returned to their nests after nocturnal activities. Thus, probably, most fleas in nests would be seeking a meal in the morning, when boxes were inspected, rather than later. Furthermore, trapped hosts probably lost more fleas than they acquired. Whenever rodents in nests were more heavily infested than those trapped, a correction was made to augment the flea population in nests (Haas, 1966*b*).

The number of *R. exulans* trapped during February–June 1962 was too low for statistical probability of a real difference between high and low mean numbers of fleas. But the sample mean is probably near the population mean because correlation of the monthly (November 1961–March 1963) mean number of fleas per trapped rat was very strong ($P < .001$), with the flea index calculated after adding numerous marked rats (see parenthetical data, Table 1). Two years earlier, under comparable conditions during growth of the previous cane crop, the trends of the mean were identical except that no low occurred in September.

Changes in the sex ratio of fleas in rat nests suggested that the August–October decline (Fig. 2) was caused more by disappearance of male fleas than by an increase in female fleas. With low population densities, subtraction of males in the interest of homogeneity reduces sample sizes when larger samples are also desired.

Except for small numbers found before May 1962, *X. vexabilis* males always outnumbered females in *M. musculus* nests probably because this host is not as suitable as *R. exulans*. Morlan (1955) reported evidence that male fleas predominate on secondary hosts. Experimentally, Haas (1965*a*) found that progeny of *Xenopsylla cheopis* (although not *X. vexabilis*) from females fed on house mice included significantly more males than females.

Eskey (1934) found that among *X. vexabilis* on *R. exulans* trapped in the Hamakua District, 43% were males, only 5% less than in field 101b rat nests. Mice in boxes and traps and rats in traps were infested with too few fleas to give reliable sex ratios. The higher counts on rats in nests had ratios that were in general similar to those of adult fleas living in the nests.

In general, when considering the total flea population, an increasing density with a comparatively high percentage of males indicates that natality exceeds mortality, and a decreasing density with a comparatively low percentage of males indicates that mortality exceeds natality. At higher latitudes, as in Wisconsin (Haas and Dicke, 1959), where there is one short season of intense breeding, this reversal of sex ratio with rise and fall in population density is easier to detect than in Hawaii, where breeding is continuous and generations tend to be extensively overlapped.

Removal of fleas from live-trapped mice did not significantly depress the mean because the mean number of fleas on unmarked hosts was so low. In some samples only marked mice were infested. Evans and Freeman (1950) reported that recaptured hosts could become infested with as many as or with more fleas than they had only 24 hours earlier. *R. exulans,* however, did not become reinfested to the level recorded at first examination. It would have been preferable to replace fleas on trapped rats.

Herbicides applied to weeds in the cane field in February 1962 might have repelled some rodents and killed some fleas. But this interpretation can be questioned because the application of herbicide was made when the populations were at or near the bottom of downward trends outside the field (unpublished Health Dept. data) as well as inside (Table 1 and Fig. 2).

Correlations, Regressions, and Predictions

Although Stark and Miles (1962) and Layne (1963) found positive correlation between abundance or density of rodents and the mean number of fleas on trapped ones, and Haas (1966*a*) reported evidence of the same relationship between cat fleas and mongooses, no such relationship was found between either *R. exulans* or *M. musculus* and *X. vexabilis*. Furthermore, only with the mouse was there a

correlation of host abundance (in traps) with the mean number of fleas in nests, but the relationship is between concurrent variables, and significance seems too low ($.01 < P < .02$) to suggest high value for predictions. Nevertheless, the major objective of this study seemingly was attained with *R. exulans*. As shown in Figure 3, the mean number of fleas in active rat nests was highly significantly correlated with the mean number of fleas per rat live-trapped the previous month. For every increase or decrease of one flea per rat, there was on the average a corresponding increase or decrease of eight fleas per nest during the following month.

Biological significance of the correlation and regression (Fig. 3) is puzzling to assess. First, because nests are probably prime sites of flea breeding, the mean number of fleas per trapped rat (Fig. 2) would be more closely related to the mean number of fleas in active nests one month later if an adjustment is made for the mean number of rats in the nests (from data in Table 1). The resulting index ($= \bar{x}$ fleas/trapped rat $\times \bar{x}$ rats/active nest) could be considered an estimate of the most actively breeding fleas per active nest. But most adult fleas found living in nests had fed at least once, and so, without a correction factor as might have been derived through the method of introduction of radioactive isotopes into hosts (Novokreshchenova and Kuznetsova, 1965), it is not surprising that this breeding index does not correlate significantly with the mean number of fleas either on trapped rats or in nests. The basic difficulty stems from heterogeneity of the count data, an ever-shifting mixture of parents and progeny, of cause and effect.

As Sazonova (1965) and Wellington (1957) might have concluded, more quantitative data (indices) are not as much needed as qualitative data on individuals. Behavioral and physiological considerations, especially those that pertain to feeding and breeding activities in nests, cannot be estimated with much precision from routine flea indices even if they are refined (e.g., to counts of gravid females), for such data collected under the equable Hawaiian temperatures are not very informative. Natality depends on many variables, especially quality of the host (Haas, 1965*a*). If time had permitted, measurement of oviposition (and natality) by isolating females for a standardized period (Seal and Bhattacharji, 1961) would have provided some quantitative data valuable for an insight into reproductive quality of individuals and the populations they form. Dissection, a technique that can yield precise estimates of physiological age (Klein, 1966), could not, of course, be used with the technique of sampling with replacement.

Another measure of natality, the mean number of 3rd instar larvae per gravid flea, should have been calculated from counts of larvae in nests. But only the presence or absence of larvae could be recorded. Yet these data showed that the percentage of active rat and mouse nests infested with larvae (probably mostly *X. vexabilis*) correlated very strongly ($P < .001$) with the percentage infested with adult *X. vexabilis*.

Compared with rat-nest-flea relations, population densities of mice in nests, especially occupied nests (Fig. 4), were very closely related to mean numbers of fleas in nests (Tables 2 and 3). But these relationships are of no value in predicting how many fleas there will be in mouse nests a month hence. In addition, correlation of mean numbers of live-trapped mice and active mouse nests was not nearly as strong as that of *R. exulans* with its active nests. Nevertheless, the three flea indices (Fig. 2) from mice (bodies and nests) correlated significantly with corresponding indices from rats. But differences in host population densities and flea sex ratios suggest correlations were coincidental.

Figure 4 illustrates a relationship between host and breeding site of flea that is probably basic in the ecology of most if not all fleas whose larvae inhabit nests or other resting places of the hosts. The nature of the relationship varies depending on host ecology and behavior; for example, intraspecifically, solitary male bats have fewer fleas than colonial females and young (Hůrka and Hůrka, 1964), and multinest female moles have fewer fleas than uninest males (Smit, 1962).

Although mean monthly soil temperatures (Haas, 1965*b*) do not correlate with any of the full-term data on the flea population from field 101b, a study (Health Dept. data) of *X. vexabilis* in 122 *R. exulans* nests removed during July 1961–September 1964 from burrows in a variety of other localities at elevations of 152–

305 meters in the enzootic plague area yielded pooled data which indicated that the mean number of fleas was distinctly higher in summer (May–September) than in winter (October–April). The high was 10.7 in June (compare with the peak of 10.4 shown in Figure 2); the low was 2.1 in January. Accompanying data include neither mean number of rats per nest nor mean number of fleas per rat. Hence, relationships of these important variables to mean numbers of fleas in nests cannot be determined.

Data from field 101b, particularly the monthly increase in mean numbers of fleas per rat nest from October through January (Fig. 2) and the concurrent monthly decrease of soil temperatures (Haas, 1965*b*), are evidence that the annual temperature cycle had little if any direct influence on flea populations. Evidently the influence was primarily indirect via the hosts: fluctuations in population densities in nests (concurrent with rats, delayed with mice) had a much more direct influence on flea populations. Although flea breeding was favored by increased numbers of rodents in nests regardless of season, the problem remains of explaining why in winter the mortality of males increased relative to that of females, as is suggsted by the difference between sex ratios in summer and winter. No experimental data are available on effects of constant temperatures of 19°C and lower on the development and mortality of immature stages of *X. vexabilis* males. It has been shown in unpublished laboratory studies referred to by Cotton and Griffiths (1967) that differences of only 4°C, especially at lower ambient temperatures, altered greatly the behavior and the length of the life cycle of vole fleas. It would be valuable to compare similar data for *X. vexabilis* since the mean monthly temperatures in the cane field studied here varied by only 4.5°C (19°–23.5°C) (Haas, 1965*b*).

For predictive purposes the ratio of the mean number of fleas on trapped rats to the mean number of fleas in rat nests a month later is more useful than the ratio of the first index to the total flea index for rats a month later. Smaller variances and the significant mean difference between ratios of increasing and decreasing indices suggest consistent relationships useful for predictions. Mathematically the ratios are governed by a property of ratio-type variables that converge as they decrease in value and diverge as they increase. Explanation of underlying biology is difficult because inadequate behavioral and physiological assessments obscure reasons for increase of fleas on hosts in traps one month before increase of fleas in nests. Superficially, the decrease in mean number of hosts per nest (from data in Table 1) could have contributed to the lag in increase in mean number of fleas per trapped host (Fig. 2). But there are probably significant changes in *X. vexabilis* behavior and physiology that are independent of the host but dependent on the individual flea itself (physiological age) and on population densities of its own species. In a study of the European chicken flea, for example, Humphries (1967) explained why crowding in the nest or on the host increases the rate of copulation.

Cole and Koepke (1947) discussed problems of interpretation resulting from the heterogeneity in flea data from trapped rodents. Interpretation of flea data from nests of individual rodent species is also complicated by heterogeneity because numerous combinations of all ages and both sexes of hosts can inhabit each particular nest for variable portions of time during its use. The breeding and survival of *X. vexabilis* depend on quality, that is, the age and sex of individual *R. exulans* in the nest (Haas, 1965*a*). Although differences would not be as extreme as Krampitz (1965) found in the case of the mouse flea on house mice, it is desirable to measure effects of different quantities of *R. exulans* (and *M. musculus*) sequentially and simultaneously in simulated nests. Family groups, in particular, deserve study.

In conclusion, flea and rodent data from field 101b cane crop of 1961–1963 are suggestive evidence of possible practical as well as probable basic relationships, but until further research can be done, especially during a period of high rodent population densities in cane fields, recommendations are to forego predictions and to include rat and mouse nests from both nest boxes and burrows in the plague surveillance program in Hawaii.

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